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Research article

Response on root regrowth potential to soil moisture in Sedum species during winter in Særheim, Norway

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ABSTRACT

Purpose: The impact of winter moisture on root metabolism and root integrity has potential consequences for the geographical distribution of drought-adapted succulent species and for their long-term performance on green roofs. The interacting effects of soil characteristics and precipitation frequency on root mortality under winter conditions and the potential to grow new roots in spring were evaluated for six *Sedum* species under controlled conditions.
Methods: To test for the impact of soil moisture during winter on root regrowth potential in six Sedum species, we used a combination of two substrates with differing water-holding capacity and four contrasting watering regimes. Specially, for the fine and coarse substrates, total pore volume was 42 and 46 %, respectively, and maximum water-holding capacity (i.e. field capacity) was 0.50 and 0.33 kg water per L, respectively. The four watering treatments involved overhead watering to runoff (approx. 10 mm): once every second week, once a week, three times per week and three times per week with 1 cm standing water in trays from January to March 2019.
Results: It was found that winter soil moisture had no major impact on root mortality or root regrowth potential in spring. Root mortality was not affected by watering frequency and regrowth potential showed no directional response to increased watering frequency, although species-specific responses were involved. Root diameter did not differ between the substrates, but there were some differences between the species. *Sedum rupestre* had on average the thickest roots (0.17 mm), followed by *S. acre*, *S. anglicum* and *S. sexangulare* (0.15–0.16 mm), while *S. album* and *S. hispanicum* had the thinnest roots (0.12–0.13 mm). Moreover, effects of watering frequency on root mortality and regrowth potential were not influenced by soil water-holding capacity across species. We concluded that winter soil moisture had no negative effects on root performance within the range of treatments tested here.
Conclusions: Root response to transient waterlogging or moist but unsaturated soil may not be an important mechanism for determining the survival and distribution of temperate *Sedum* species during winter.

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1. Introduction

Leaf succulents such as *Sedum* species are adapted to periodic water shortages through morphological and physiological adjustments that conserve water, but their root system is not succulent and is usually small and shallow [1]. These adaptations make most *Sedum* species weak competitors for nutrients and light when water is not limiting growth. This restricts their distribution to dry habitats or to microhabitats on shallow soils in regions with higher precipitation [2,3]. In wet and cold regions, only a very few succulent species occur naturally. These patterns may be the result of competitive hierarchies, but trade-offs between adaptations to tolerate summer drought episodes and contrasting winter conditions such as low temperatures, repeated ice formation in the soil and prolonged periods of wet soil may also be involved.

Elevated soil moisture during winter can affect root and shoot performance. Waterlogging during the winter months can lead to reduced gas exchange, anoxia, and the accumulation of phytotoxic compounds, which can negatively impact root health and function. In extreme cases of soil waterlogging, gas exchange is reduced, causing anoxia and build-up of ethylene, CO_2 and organic acids [4]. The *Sedum* relative *Phedimus middendorffianus* shows some tolerance to soil waterlogging during growth [5], but responses may be species-specific and differ with season. These processes may be less of a problem under cold conditions, when respiration rates are lower and oxygen solubility in water is higher [6,7].

Studies have shown that the frost hardiness of cold-acclimated temperate *Sedum* species is often around −20 °C and below [8]. However, these studies do not distinguish between root and shoot responses. From studies in forest systems, it is known that frozen ground and soil freeze-thaw cycles result in high fine root mortality [9,10], but the impact probably differs between species and freeze-thaw regimes [11]. Moreover, previous studies have all been performed on deep soils and, while similar responses can be expected in shallow soils, presumed differences in energy balances, freeze-thaw cycles and freezing patterns make it difficult to predict potential physical and physiological damage to *Sedum* fine roots [12]. Hence, how roots of succulent species such as *Sedum* respond to winter soil moisture and the impact of these responses remain open questions.

The widespread use of *Sedum* vegetation on extensive green roofs, with challenging abiotic conditions in both summer and winter [13], adds a practical dimension to these research questions. Shallow substrates on green roofs provide less buffering of temperature and soil moisture than deeper soils. Hence, succulents are the most commonly used green roof vegetation [14], as they are highly adapted to the dry environments on roofs [15]. However, green roof technology for stormwater management is increasingly being transferred to cold, wet regions where periodically high soil moisture content can be expected even in shallow roof substrate profiles. Observations indicate that the winter phase or the transition from winter to spring is critical for *Sedum* performance in the shallow soils of green roofs in both cold wet regions [13] and cold dry regions [16]. Root performance may be an important component of these observed responses.

To determine whether winter soil moisture is a critical factor for *Sedum* performance, we designed a study to evaluate the effects of substrate characteristics and precipitation frequency under winter conditions on root mortality and regrowth potential of *Sedum* roots. We addressed two main questions: (1) Does winter soil moisture have such a strong negative effect on root metabolism and integrity that root mortality increases and the potential to grow new roots in spring is constrained? (2) To what extent are these responses to watering frequency affected by the water-holding capacity of the soil?

2. Material and methods

2.1. Experimental design

To test for the impact of soil moisture during winter on root regrowth potential in six *Sedum* species, we used a combination of two substrates with differing water-holding capacity and four contrasting watering regimes. The experiment was run in winter 2019–2020, using the facilities of the Norwegian Institute of Bioeconomy Research at Særheim Research Centre, SW Norway (lat. 58.761034, long. 5.651822).

2.2. Substrate composition

We prepared a fine substrate and a coarse substrate by combining different size fractions of pumice. The fine substrate had 40 % 0–2 mm and 34 % 2–5 mm pumice, while the coarse substrate had 26 % 2–5 mm and 47 % 5–10 mm pumice. In addition, both mixtures had 9 % sieved, mature, nutrient-poor compost and 17 % gravel (3–5 mm). All proportions were measured per volume and all substrates were blended for 2 min in a concrete mixer. For the fine and coarse substrates, total pore volume was 42 and 46 %, respectively, and maximum water-holding capacity (i.e. field capacity) was 0.50 and 0.33 kg water per L, respectively. Substrate pH, measured in a 1:5 solution with distilled water, ranged from 7.5 to 7.6. These substrates were randomly allocated to cells in small plug trays with 24 cells per tray (12 cells per substrate, 4 cm × 4 cm cell surface).

2.3. Plant material

Rooted cuttings of Sedum acre (L.), *S. album* (L.), *S. anglicum* (Hudson), *S. hispanicum* (L.), *S. rupestre* (L.) and *S. sexangulare* (L.) were transplanted to random positions in a prepared plug trays in the summer of June 2019. There were four cells per species in each tray and 12 trays in total, giving 48 plants per species. At transplanting, shoots were about 20 mm long. The prepared trays were kept in a greenhouse, watered to runoff once a week throughout the summer and moved to an unheated greenhouse for winter acclimation in

September. The selected *Sedum* species show only a small variation in their niche preferences quantified as Ellenberg indicator values (EIV), scoring high on light and low on moisture, salinity and nitrogen [17], but their geographical distribution in their native range shows some differentiation (gbif.org, [18]). For example, both *S. acre* and *S. album* are widespread in Europe on various nutrient-poor soils, while *S. sexangulare* and *S. rupestre* are also widespread, but more continental. *Sedum rupestre*, which has higher EIV for nitrogen, prefers soil that is more productive. *Sedum anglicum* has an oceanic to sub-oceanic distribution on acidic soils, while *S. hispanicum* has a central to southeastern European distribution.

2.4. Watering

The watering regimes were designed to represent a range of northern European coastal winter conditions without snow cover. Winter precipitation at the study location is around 20 mm/week, while drier locations like southern Sweden, Frankfurt and London have around 10–13 mm/week, although some of this may fall as snow in all cases. Precipitation frequency and amount increase along the western coast of Norway, where green roofs are more or less permanently wet throughout the winter. In this region, the number of rainy days per month ranges from 10 to 15 to 20–25. The watering regimes in the present study covered most of this range, including drier conditions. The four watering treatments involved overhead watering to runoff (approx. 10 mm): once every second week, once a week, three times per week and three times per week with 1 cm standing water in trays from January to March 2017. Three plug trays were used per watering treatment. The absence of wind in the greenhouse gave slower drying of the substrate than expected under field conditions. Mean air temperature 1 m above the plants was 4.2 °C during the experimental period and ranged from −7.7 to +17.3 °C (Fig. 1). This gave several days with frozen substrate and a few freeze-thaw cycles.

2.5. Harvest and root image analysis

All trays were moved to a warm greenhouse on March 1, 2020 and watered three times per week with a dilute NH_4NO_3 fertiliser solution. Three weeks later, shoots were cut at the surface, dried for 48 h at 70 °C and weighed. Roots were washed free of substrate particles and the number of root tips in subsamples was counted using a dissecting microscope with additional transmitted light at 16-40× magnification. All roots were scanned at 600 dpi in 5 mm water using a calibrated dual-beam flatbed scanner (Epson Perfection V700 Photo Scanner, Epson America Inc., CA, USA) and analyzed for total root length and root diameter using the WinRhizo software (Regent Instruments Inc., Québec, Canada). Root regrowth potential was estimated as number of root tips per unit root length for the whole root system. Some of these were old root tips, it was possible to distinguish new tips from old based on lower root transparency behind the elongation zone, these were counted with the new tips.

2.6. Statistical analyses

In the statistical analyses, the initial statistical model was a factorial ANOVA, which used species, watering and substrate as fixed factors, and plug tray as a random factor nested within the watering level. Leaving out the tray factor gave almost identical results (Table S1) and enabled the effect size of responses to the different factors to be calculated. The ANOVA models were tested with the general linear model (GLM) option in Minitab 17 (Minitab Ltd., Coventry, UK). The relationship between root diameter and root regrowth potential was evaluated with simple linear regression models for each species separately. Counts of new root tips per unit root length were log-normal transformed to correct for heteroscedasticity of residuals. Two outliers for root length and root biomass were identified by strongly deviating length to biomass ratio and were replaced with treatment means. Partial effect size was estimated as ω_p^2 [19].

In Table S1, results of ANOVA tests on the interactive effects of species (Spec), substrate composition (Sub) and watering regime (Wat) on root regrowth of Sedum species, with R^2adi of 67 % for tray treatment and 65 % of without tray treatment, respectively.

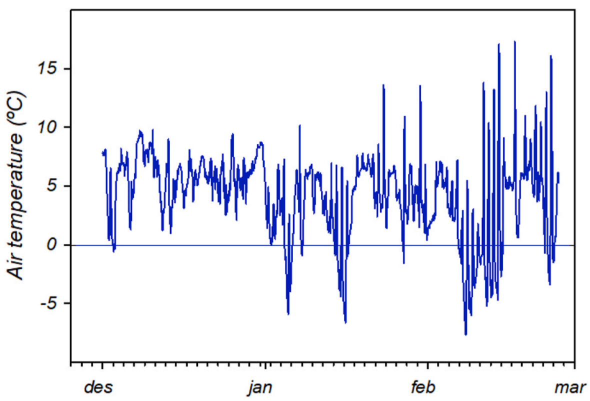

Fig. 1. Air temperature measured at 1 m above the *Sedum* plants during the winter months.

3. Results

There were differences between the six *Sedum* species tested in regrowth potential and in their response to soil moisture (Table 1). However, the responses were not consistent (Table 2, Figs. 2–3). *Sedum acre* and *S. anglicum* showed declining regrowth potential with increasing soil moisture, while regrowth potential in *S. sexangulare* showed no clear pattern with respect to moisture conditions (Fig. 2). A response in common for all species was that effects of watering treatment did not differ between the fine and coarse substrates (no interactions (Table 2). However, substrate composition affected the regrowth potential, irrespective of watering treatment, in three of the species, where the fine substrate gave slightly higher regrowth potential across watering levels (Fig. 2). *Sedum sexangulare* had the highest regrowth potential of the species, averaged over treatments, while regrowth of *S. rupestre* was much lower than in the other species (Fig. 3).

In Table 1, results of ANOVA tests on the interactive effects of species (Spec), substrate composition (Sub) and watering regime (Wat) on root regrowth potential in a set of six Sedum species. Percentage of total variation explained by the model term and effect sizes estimated as ω_p^2 are also shown. Total degrees of freedom (df) = 274, R^2adi = 65 %.

In Table 2, results of ANOVA model testing the interactive effects of substrate composition and watering regime on root regrowth potential in six Sedum species. Effect sizes estimated as $\omega_p^2$are also shown.

In Fig. 1, Root regrowth potential (log-normal transformed counts of root tips per metre fine roots; mean with 95 % confidence interval) following four contrasting watering regimes during winter in six *Sedum* species growing in a fine (white) or coarse (black) substrate. The four watering regimes involved overhead watering to runoff once every second week (1), once a week (2), three times per week (3) and three times per week with 1 cm standing water in trays (4).

In Fig. 3, comparison of root diameter (A) and root regrowth potential (B, log-normal transformed counts of root tips per metre fine roots) across *Sedum* species, averaged over treatments (mean with 95 % confidence interval). Letters indicate grouping based on Tukey pairwise comparisons controlling for the simultaneous confidence level. Means that do not share a letter are significantly different.

In *S. album*, *S. anglicum*, *S. rupestre* and occasionally *S. sexangulare*, new root tips emerged in bundles along the old roots.From left: *S. acre* (A), *S. album* (B), *S. anglicum* (C), *S. hispanicum* (D), *S. rupestre* (E), *S. sexangulare* (F). Scale bar is 10 mm (Fig. 4). This pattern was absent in *S. acre* and *S. hispanicum*. Scrutiny of close-up photos of bundles in *S. album* revealed the remains of old roots, indicating reuse of the bundle positions (Fig. 5).

Root diameter did not differ between the substrates, but there were some differences between the species. *Sedum rupestre* had on average the thickest roots (0.17 mm), followed by *S. acre*, *S. anglicum* and *S. sexangulare* (0.15–0.16 mm), while *S. album* and *S. hispanicum* had the thinnest roots (0.12–0.13 mm) (Fig. 3). The effects of watering on root diameter were not determined, as most roots were established before the start of watering treatment. We observed no dead roots, indicating low mortality of first- and second-order roots, but mortality of small higher-order roots was difficult to evaluate with our experimental design. In three of the species, there was a tendency for an increase in root regrowth potential with increasing average root diameter (Fig. 6). Relationship between average root diameter and root regrowth potential (log-normal transformed counts of root tips per metre fine roots) averaged over different combinations of winter soil moisture in six *Sedum* species. The linear relationship was only significant for *S. acre* (solid line), *S. anglicum* (short dashed line) and *S. rupestre* (long dashed line). With adjusted R^2 values below 25 %, the linear regression models explained only part of the variation.

4. Discussion

The impact of winter moisture on the performance of drought-adapted succulent species has potential consequences for the geographical distribution of such species and for their long-term performance on green roofs. In this study, we found that winter soil moisture had no major impact on root mortality or on root regrowth potential in spring in a set of temperate *Sedum* species. First, we found that root mortality was not affected by watering frequency and that the regrowth potential of the species tested showed no directional response to increased watering frequency, although species-specific responses were involved. Second, we found consistently that the effects of watering frequency on root mortality and regrowth potential were not influenced by the substrate water-holding capacity across species. There were no consistent directional responses in root mortality or root regrowth potential to soil moisture as imposed by the watering frequency treatments. Moreover, these effects were not influenced by the substrate water-holding capacity across the six species tested, despite considerable differences in water-holding capacity. This indicates that winter soil moisture had no negative effect on root metabolism and integrity within the range of treatments tested here. Hence, root responses to

Table 1
Results of ANOVA tests on the interactive effects of species (Spec), substrate composition (Sub) and watering regime (Wat) on root regrowth potential in a set of six Sedum species.

	df	F	P	% of variation explained	ω_p^2
Species	5	91.88	0.000	58	0.62
Substrate	1	10.88	0.001	1	0.03
Water	3	2.02	0.113	1	0.01
Sp*sub	5	2.22	0.053	1	0.02
sp*wat	15	4.42	0.000	8	0.16
Sub*wat	3	0.46	0.713	0	−0.01
Sp*sub*wat	15	0.54	0.915	1	−0.03

Table 2
Results of ANOVA model testing the interactive effects of substrate composition and watering regime on root regrowth potential in six Sedum species.

	Substrate			Watering			Substrate * watering			
	F	P	ω_p^2	F	P	ω_p^2	F	P	ω_p^2	R^2adj
S. acre	4.71	0.036	0.06	5.22	0.004	0.24	0.15	0.927	−0.07	25
S. album	8.41	0.006	0.13	1.42	0.251	0.03	0.48	0.700	−0.04	13
S. anglicum	6.96	0.012	0.11	12.02	0.000	0.41	0.62	0.603	−0.02	44
S. hispanicum	0.15	0.702	−0.02	1.67	0.192	0.05	0.18	0.906	−0.06	0
S. rupestre	0.41	0.527	−0.01	2.50	0.073	0.09	0.56	0.644	−0.02	5
S. sexangulare	0.53	0.470	−0.01	3.58	0.022	0.15	1.07	0.374	0.11	14

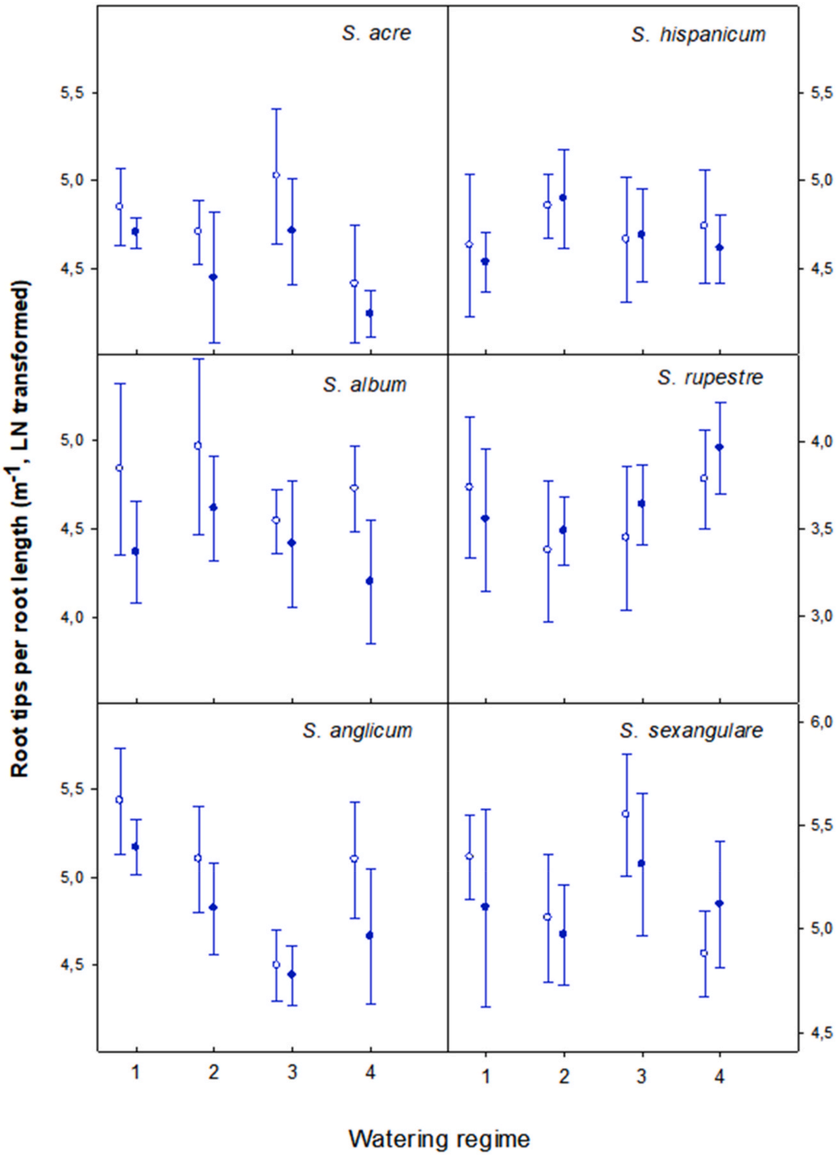

Fig. 2. Root regrowth potential.

soil moisture are probably not important in determining the winter survival and distribution of *Sedum* plants. However, it is important to bear in mind that the soil was not fully saturated in our study and that periods of high water content were transient, except for the lower parts of the plugs in the treatment with standing water.

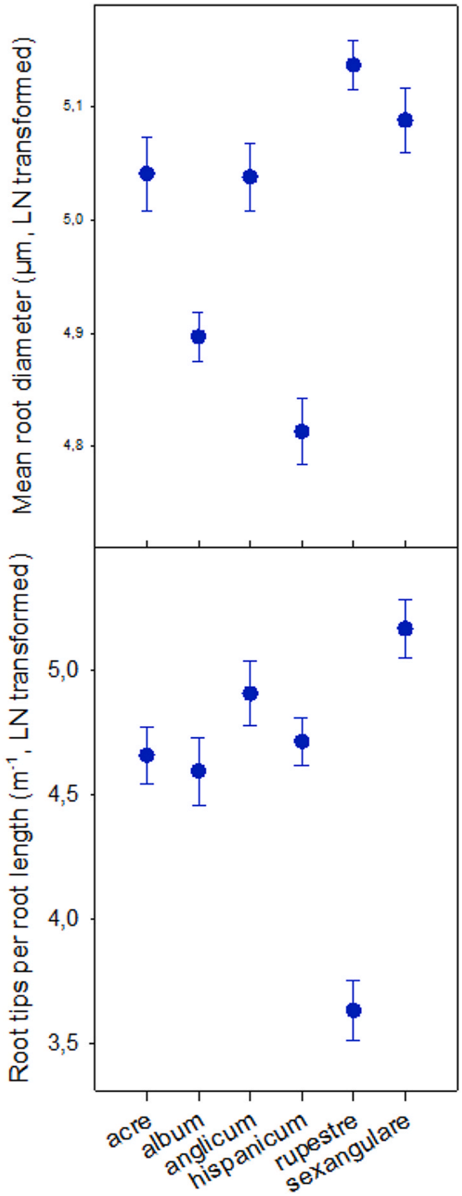

Fig. 3. Comparison of root diameter (A) and root regrowth potential (B, log-normal transformed counts of root tips per metre fine roots) across *Sedum* species.

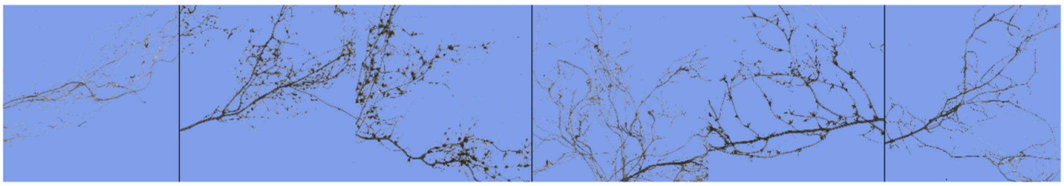

Fig. 4. Details of the root system showing the bundle pattern observed in some *Sedum* species.

4.1. No consistent response to soil moisture

The lack of response to soil moisture countered the expected increase in mortality and decline in root regrowth potential. The lack of comparable studies, both for taxa and adaptations, makes it difficult to infer whether these patterns are general or specific for these

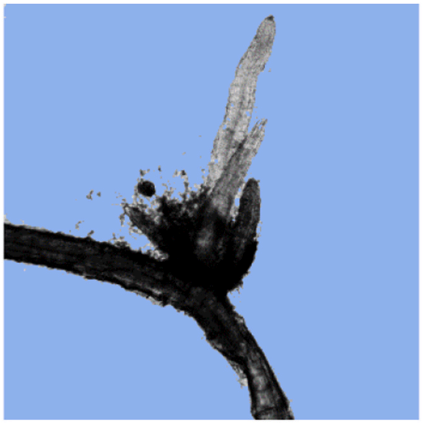

Fig. 5. Close-up of a root bundle on a *Sedum album* root. Bar = 0.15 mm.

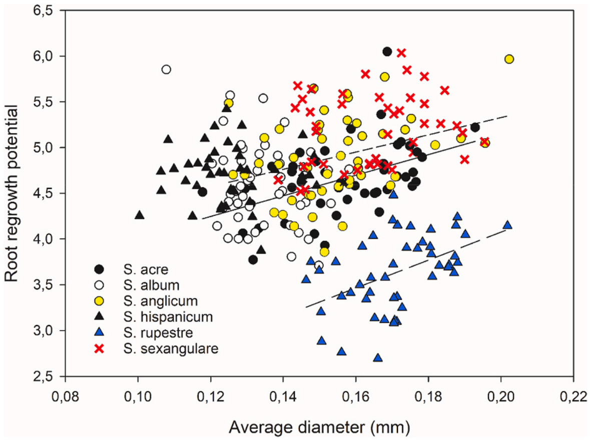

Fig. 6. Relationship between average root diameter and root regrowth potential.

species. The fact that we found only small differences between the species in terms of measured responses to soil moisture indicates that they have similar adaptations to winter soil moisture. A set of possible mechanisms could be involved in winter root damage, such as effects of anoxic or hypoxic conditions during submergence or waterlogged soil, the accumulation of phytotoxic compounds, mechanical damage during freeze-thaw cycles, direct damage from membrane disruption at low temperatures and elevated risks of pathogen infections [10,20,21]. However, few of these mechanisms were in action during our experiment. Although roots are less hardy than shoots, direct damage to root functions caused by low temperatures is less likely at the temperatures observed in our study. Freeze-thaw cycles have been observed to cause root injury in species such as *Holcus lanata* and *Calluna vulgaris* at moderate soil temperatures of above −10 °C [11], but this process may need larger volumes of soil to create enough force to disrupt roots [22]. We observed no pathogens, so the major mechanism expected was the potential effects of transient water-saturation on substrate gas exchange with shortage of O_2 and accumulation of ethylene, CO_2 and organic acids [4]. As water use by *Sedum* under cold winter conditions is marginal, evaporation from the substrate was the main factor driving water loss. Hence, soil moisture was determined by the pattern of water addition, irrespective of substrate characteristics. The fine and coarse substrates had similar porosity (42 and 46 %) and, although we observed contrasting wetness between substrates and treatments during the experiment, the differences in water-holding capacity (0.50 compared with 0.33 kg water per L substrate) were not sufficient to affect root functions. We ascribe this lack of response to increased watering frequency to the high porosity of the substrates, which was sufficient for gas exchange in all treatment combinations, the increased solubility of O_2 in water and lowered root respiration at these low temperatures.

4.2. Species differed in trait means

Differences between species dominated the observed patterns of root regrowth potential. There were no strong indications that these differences were related to the native habitats of the species. Rather, they showed more of a phylogenetic signal, with *S. rupestre* having considerably lower root regrowth potential than the other species. The phylogeny of Crassulaceae and the large *Sedum* genus is in part unresolved [23]. *Sedum rupestre* is often placed in the *Petrosedum* genus [24] in the Sempervivum clade within the Crassulaceae, while the remaining species used in our study are from the more closely related Acre and Leucosedum clades and Anglica series. In this case, the difference in root regrowth potential correlated with phylogenetic distance. We expected *S. anglicum* to stand out as the most tolerant to soil moisture, as it inhabits coastal areas with high winter moisture, in contrast to the more arid conditions experienced by species like *S. album* and *S. hispanicum*. This was not the case, however. Instead, *S. anglicum* showed a tendency for a stronger decline in root regrowth potential at increasing soil moisture compared with the other species. As root mortality was negligible, we were unable to test for differences in root mortality between species.

4.3. Potential persistent and fast-cycling units

Presence of persistent and fast-cycling units of root turnover is known for trees and has now been documented in perennial herbaceous plants [25] and even in desert systems [26]. This information is interesting concerning the root clusters we observed in some *Sedum* species. These clusters could indicate fast-cycling units formed repeatedly from the same positions on more persistent roots over time, but this has to be investigated further to document mechanisms and functions.

Based on the persistence-fast cycling concept, the potential for initiation of new roots could be related to root longevity and to longer-lived roots having greater potential for root initiation in spring. This would also imply a seasonal pattern of decay of the fast-cycling parts. As root longevity has been found to increase with root diameter in some studies [27,28], we expected root regrowth potential to increase with mean root diameter. We found no simple relationship between root diameter and root regrowth potential, but the few significant relationships we found indicated an increase in root regrowth potential with root diameter. However, our dataset was small and the range of mean root diameter observed was narrow. Even the thickest *Sedum* roots can be considered fine roots, but at present little is known of their turnover and longevity.

4.4. Limitations

The study mainly focused on root mortality and regrowth potential to the soil moisture conditions. For other aspects of root performance, such as root architecture, nutrient uptake, or interactions with soil microorganisms, which could also be influenced by winter soil moisture conditions, will be conducted in further studies. In addition, during the statistical analysis, using the ANOVA models in this study is the reliance on the general linear model (GLM) option in Minitab 17 for analysis. While ANOVA is a widely-used statistical technique for comparing means across multiple groups, its application within the GLM framework may introduce certain constraints and assumptions that could affect the interpretation of results. To address these limitations, conducting sensitivity analyses or exploring alternative statistical approaches should be considered to corroborate the findings in the future studies. Additionally, transparently reporting any deviations from ANOVA assumptions and detailing the rationale behind the choice of analysis software can enhance the transparency and credibility of the study.

5. Conclusion

To conclude, soil moisture changes due to varying frequency of watering and the water-holding capacity of the two substrates tested had no major impact on winter root mortality or the ability to grow new roots in spring in six *Sedum* species. Hence, transient waterlogging or wet, but unsaturated, soil during winter is not likely to be an important factor in determining *Sedum* winter survival and distribution. However, for a better understanding of root growth dynamics in *Sedum* species, further investigations are needed on root turnover and plasticity. These findings will provide useful guidelines to roof greenery management and resilient species selection. Therefore, roof greening should emphasize the characteristics of extensive management, low maintenance costs, and easy survival. This will be of crucial practical significance in urban greenery.

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Data availability

The datasets generated or analyzed during this study are available from the corresponding author on reasonable request.

CRediT authorship contribution statement

Peng Ji: Writing – original draft, Conceptualization. **Yuan Chan:** Data curation. **Mingyue Lu:** Data curation. **Ying Zhai:** Data curation. **Hailiang Lv:** Writing – review & editing. **Hongyi Wang:** Data curation. **Hans Martin Hasnslin:** Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e36077.

Appendix

Table S1
Results of variance analyses (ANOVA) with and without plug tray nested within water level as a factor in the statistical models. Note, Sp refers Species, sub refers Substrate, wat refers Water.

	With tray			Without tray		
	df	F	P	df	F	P
Species	5	97.11	0.000	5	91.88	0.000
Substrate	1	11.40	0.001	1	10.88	0.001
Water	3	0.87	0.497	3	2.02	0.113
Sp*sub	5	2.48	0.033	5	2.22	0.053
Sp*wat	15	4.61	0.000	15	4.42	0.000
Sub*wat	3	0.46	0.708	3	0.46	0.713
Tray(W)	8	2.52	0.012			
Sp*sub*wat	15	0.59	0.879	15	0.54	0.915
R^2 adj		67			65	

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